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MORPHOLOGY OF SOME LORICATE HETEROTROPHIC SPECIES OF FLAGELLATE (CHOANOMONADA, BICOSOECIDA, JAKOBIDA), WITH EMPHASIS ON TAXONOMICAL PROBLEMS OF ASEXUAL PROTIST SPECIES

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Morphology of some Loricate Heterotrophic Species of Flagellate (Choanomonada, Bicosoecida, Jakobida), with Emphasis on Taxonomical Problems of Asexual Protist Species. Tikhonenkov D. V., Mazei Yu. A., Mylnikov A. P., Kireev A. V. — Morphology of the some loricate heterotrophic flagellate species in the natural and clonal populations are investigated. Differential diagnoses and descriptions of species are provided. Some taxonomic problems of loricate heterotrophic flagellates and protists identification are discussed. A new replacement name *Salpingoeca skujae* Tikhonenkov et Mazey, nom. n. for *Salpingoeca urnula* Skuja, 1948, nom. praeocc., non *Salpingoeca urnula* Korshikov, 1926 is proposed.

Key words: morphology, heterotrophic flagellates, species descriptions.

Морфология некоторых видов домиковых гетеротрофных жгутиконосцев (Choanomonada, Bicosoecida, Jakobida) и таксономические проблемы идентификации агамных протистов. Тихоненков Д. В., Мазей Ю. А., Мыльников А. П., Киреев А. В. — В природных популяциях и клональных культурах исследована морфология некоторых видов гетеротрофных флагеллят, имеющих домики. Приведены дифференциальные диагнозы и описания видов. Обсуждаются некоторые таксономические проблемы идентификации домиковых гетеротрофных жгутиконосцев и других протистов. Представлено новое замещающее название *Salpingoeca skujae* Tikhonenkov et Mazey, nom. n. для *Salpingoeca urnula* Skuja, 1948, nom. praeocc., non *Salpingoeca urnula* Korshikov, 1926.

Ключевые слова: морфология, гетеротрофные жгутиконосцы, описания видов.

Introduction

Various loricate heterotrophic flagellate (LHF) are among the most abundant groups in the freshwater and marine ecosystems (Tong, 1997; Zhukov, 1978). Some species of choanoflagellates, bicosoecids, chrisomonads and *insertae sedis* have a lorica.

The LHF species are differ mainly by thecal or lorical structure (Kristiansen, 1972; Zhukov, 1993; Zhukov, Karpov, 1985). The majority of the species of these organisms was described in XIX and in the first half of XX century (e. g. Kent, 1880; Griessmann, 1914; Lemmermann, 1914). However, recently their taxonomy is in urgent need of clarification and revision (Tong, 1997).

Material and methods

Morphological characters of eight species of LHF are studied. Three natural populations and seven clonal cultures from freshwater and marine biotopes of Russia and Ukraine are examined. Morphometric measurements for fifty specimens of each species are made.

For microscopical observations, Biolam-I compound microscope equipped with phase contrast and water immersion objectives was used.

Results

Descriptions of studied LHF species are presented below. Basic biometrical characteristics of the investigated species are shown in the table 1.

Table 1. Biometric characterization of the investigated species, μm
Таблица 1. Биометрическая характеристика исследованных видов, мкм

Character	*S. pixidium*		*S. urnula*		*B. exilis*			*B. griessmanni*		
	Ld	**Ad**	**Ld**	**Ad**	**Ll**	**Lb**	**Ab**	**Ll**	**Lb**	**Ab**
x	7.29	3.86	8.81	3.22	10.82	5.64	3.69	10.64	5.32	3.83
Max	8.56	5.4	12.0	4.5	13.9	7.1	5.2	13.4	7.0	5.2
Min	5.8	2.6	6.8	2.5	7.9	3.6	2.5	7.1	3.2	2.5
SD	0.63	0.62	0.87	0.45	1.56	0.80	0.66	1.48	0.97	0.69
SE	0.09	0.09	0.12	0.06	0.22	0.11	0.09	0.21	0.14	0.10

Character	*L. globulosa*		*R. americana*		*B. lacustris*			*H. aroides*		
	Ld	**Ad**	**Ld**	**Ad**	**Ll**	**Lb**	**Ab**	**Ll**	**Lb**	**Ab**
x	6.34	3.28	8.98	11.50	11.53	6.20	3.98	10.83	5.63	7.86
Max	8.4	4.6	10.9	15.4	15.9	7.5	5.2	14.3	8.6	11.6
Min	5.0	2.5	4.8	7.9	7.9	4.5	2.9	7.1	3.9	4.3
SD	0.74	0.43	1.20	2.01	2.16	0.63	0.58	1.61	1.11	1.57
SE	0.10	0.06	0.17	0.28	0.31	0.09	0.08	0.23	0.16	0.22

Ld — lorica diameter; Ll — lorica length; Lb — lorica breadth; Ad — aperture diameter; Ab — aperture breadth. x — arithmetic mean; Min — minimum; Max — maximum; SD — standard deviation; SE — standard error of mean.

OPISTHOCONTA

CHOANOMONADA

SALPINGOECIDAE

Salpingoeca James-Clark, **1868**

Solitary heterotrophic flagellates, often attached to substrate. Cells located in organic theca with front (upper) aperture. Theca monolayered, without visible fibrillar structures. One protoplasmic collar laterally encircling base of single flagellum. Number of tentacles in collar species-specific and usually calculated with use of transmission electron microscope (Zhukov, Karpov, 1985). Spherical or oval cysts with fine membrane formed inside theca (Galaway, Lackey, 1962). However, cysts not observed in this study.

Salpingoeca pixidium Kent, 1880 (fig. 1, A, B).

Theca obovate, colorless, with more pointed end attached to substrate. Theca diameter 6—9 μm, aperture diameter 3—5 μm. Theca not close-fitting to cell. Flagellum about 2.5 times as long as cell. Nucleus situated at anterior half of cell; contractile vacuole located in cell basal part.

Found in the pond plankton and treatment plants (Borok, Yaroslavskaya Oblast, Russia). Observed in fresh waters (Kent, 1880). Noted from treatment plants (Tikhonenkov, 2006) and in stagnant reservoirs on filamentous algae, and often attached to *Dinobryon* and *Melosira* in plankton (Zhukov, Karpov, 1985).

According to Lemmermann (1914) theca very small pedicel, whith not observed in our study.

Salpingoeca skujae Tikhonenkov et Mazei, **nov. n.** (fig. 1, C, D).

(= *S. urnula* Skuja, 1948 non *Salpingoeca urnula* Korschikov, 1926)

E t y m o l o g y. The new replacement name is in honour of H. Skuja, who described this organism as *S. urnula* in 1948.

D i a g n o s i s. Theca cylindrical with roundish base; truncate anteriorly, 7—12 μm in diameter. Aperture diameter 2.5—4.5 μm. Theca wall brown. Three to ten short and

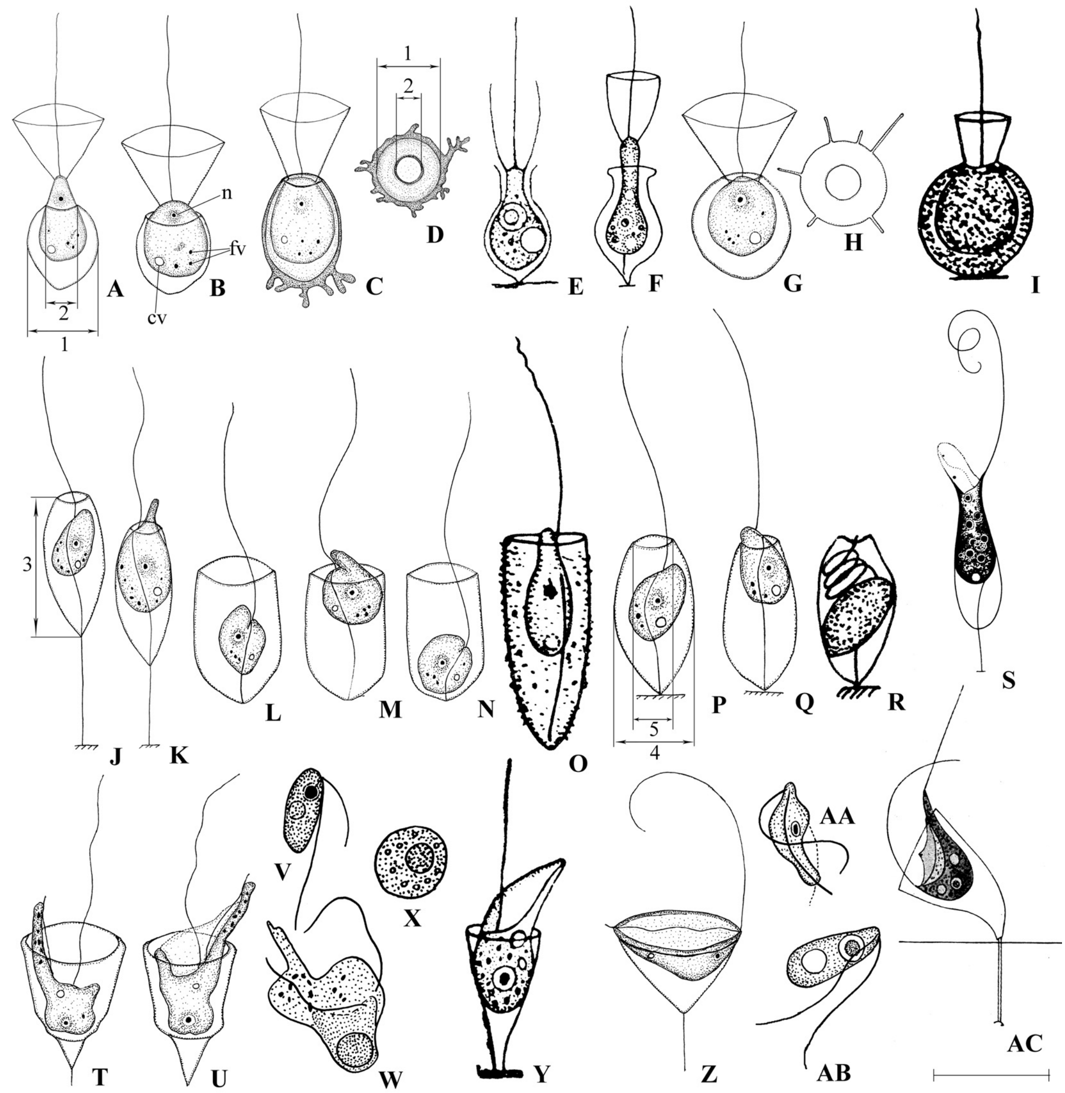


Fig. 1. Morphology of loricate heterotrophic flagellates: A, B — *Salpingoeca pixidium*; C, D — *S. urnula*; E — *S. urnula* Korshikov, 1926 (after Korshikov, 1926); F — *S. napiformis* (after Lemmermann, 1914); G, H — *Lagenoeca globulosa*; I — *Salpingoeca minor* (after Zhukov, Karpov, 1985); J, K — *Bicosoeca exilis*; L–N — *B. griessmanni*; O — *B. cylindrica* (after Lackey, 1939); P–R — *B. lacustris*; S — *B. kepreni* (after Reynolds, 1927); T–X — *Histiona aroides* (T, U — attached cells, V–X — floating forms and cyst (after Mylnikov, 1984)); Y — *H. velifera* (after Voigt, 1902); Z–AB — *Reclinomonas americana* (Z — attached cell, AA, AB — floating forms (after Mylnikov, Mylnikova, 2007)); AC — *R. campanula* (*Histiona campanula* after Penard, 1912). 1 — lorica diameter; 2 — aperture diameter; 3 — lorica length; 4 — lorica breadth; 5 — aperture breadth. n — nucleus; cv — contractile vacuole, fv — food vacuole. Scale bar 10 μm for all figures.

Рис. 1. Морфология домиковых гетеротрофных флагеллят. A, B — *Salpingoeca pixidium*; C, D — *S. urnula*; E — *S. urnula* Korshikov, 1926 (по: Korshikov, 1926); F — *S. napiformis* (по: Lemmermann, 1914); G, H — *Lagenoeca globulosa*; I — *Salpingoeca minor* (по: Жуков, Карпов, 1985); J, K — *Bicosoeca exilis*; L–N — *B. griessmanni*; O — *B. cylindrica* (по: Lackey, 1939); P–R — *B. lacustris*; S — *B. kepreni* (по: Reynolds, 1927); T–X — *Histiona aroides* (T, U — прикрепленные клетки, V–X — плавающие формы и циста (по: Мыльников, 1984)); Y — *H. velifera* (по: Voigt, 1902); Z–AB — *Reclinomonas americana* (Z — прикрепленная клетка, AA, AB — плавающие формы (по: Мыльников, Мыльникова, 2007)); AC — *R. campanula* (*Histiona campanula* по: Penard, 1912). 1 — диаметр домика; 2 — диаметр устьевого отверстия; 3 — длина домика; 4 — ширина домика; 5 — ширина устьевого отверстия. n — ядро; cv — сократительная вакуоль, fv — пищеварительная вакуоль. Масштабная линейка 10 мкм.

thick often bipalmate brown “spurs” by means of which theca attached to substrate arising radial and irregularly from thickened basal part of theca as cell senescences. Cell not occuping whole theca. Collar slightly shorter than cell. Flagellum about twice as long as cell. Nucleus and contractile vacuole almost indistinguishable due to coloured theca.

S. urnula Skuja, 1948 is younger homonym of *Salpingoeca urnula* Korschikov, 1926, and new replacement name is proposed for it. *Salpingoeca urnula* Korschikov, 1926 is characterized by the urn-shape theca about 11.5 m long, with utricular wide-elliptical posterior part, slightly tapered to short pedicel in basal end whereby organism is attached to substrate. Posterior part of the theca abruptly turning into wide and short cylindrical neck with above dilatation. Collar about as long as theca; but flagellum slightly longer than theca (Korschikov, 1926).

This species was found among the Volga River periphyton (Zhukov, 1979). Evidently, two species considerably differing on the thecal and cell morphology were described under the same names. Furthermore, we suppose that the organism described by Korshikov to be referred to *Salpingoeca napiformis* Lemmermann, 1914 (fig. 1, F), because these species have almost no morphological differences. *S. urnula* Korschikov, 1926 might appear to be a synonym of *S. napiformis* Lemmermann, 1914. But this needs further verification.

Locality. This species was found in the pond plankton samples (Borok, Yaroslavskaya Oblast, Russia). If frequently occurred in stagnant reservoirs (Zhukov, Karpov, 1985), observed in plankton of the Rybinsk Reservoir (Zhukov, 1993) and small water bodies of Yaroalavskaya Oblast. The cells quite often are attached to phytoplankters *Microcystis aeruginosa* (Kützing, 1833) Kützing, 1846 and *Fragillaria crotonensis* Kitton, 1869 (Skuja, 1948).

Lagenoeca Kent, 1880

Solitary heterotrophic flagellates in colourless or brown theca, differing from *Salpingoeca* by absence of pedicels and cytoplasmic projections in basal part of theca. Some species have thick permanent projections, which do not contribute to fixation of theca on substrate.

Lagenoeca globulosa Francé, 1897 (fig. 1, G, H).

Theca thin-walled and transparent, globe-shaped, 5–8 μm in diameter, truncated anteriorly. Aperture diameter 2.5–4.5 μm. Cell roundish, not occupying whole theca. Flagellum twice as long as cell. Nucleus located in anterior part of cell, contractile vacuole in posterior one. Long transparent radial projections can originate from basal theca part.

Found in the pond plankton samples (Borok, Yaroslavskaya Oblast, Russia). Occurs in clear stagnant reservoirs (Zhukov, 1993).

Zhukov and Karpov (1985) noted larger lorica size in this species (10 μm). *L. globulosa* is very similar to *Salpingoeca minor* Dangeard, 1910 (fig. 1, I) in morphological features, but distinguished by transparent theca and presence of the projections in the basal lorica part. It differs from other representatives of the genus *Lagenoeca* it differs by the globular shape of the lorica.

CHROMALVEOLATA

STRAMENOPILES

BICOSOECIDA

Bicosoeca (James-Clark, 1868) Stein, 1878

Solitary or colonial heterotrophic flagellates with organic lorica and two retractable flagella. Shape and lorica-wall structure species-specific (Kristiansen, 1972). Tip of pos-

terior flagellum attached to cell at bottom of lorica; anterior flagellum free and taking part in feeding. Anterior flagellum retracting and coiling up rapidly on front end of cell when disturbed. Posterior flagellum retractible too, and cell driving into the bottom of the lorica. Anterior part of the cell leaning out of lorica and food perceptive lip forming on it when the organism undisturbed and feeding.

Straightened after retract, anterior flagellum makes slow undulating movements with large amplitude at first, afterwards highly rapid, consequently undulations become invisible. All species are filterers and capture bacteria or eukaryotic algae. The cell multiplies by longitudinal division in two. The cysts are not produced except in *B. mitra* (Zhukov, 1993).

Bicosoeca exilis Penard, 1921 (fig. 1, J, K).

Solitary. Lorica attached to substrate by fine pedicel; pedicel length varying from 0.5 to 1.0 times of cell length. Lorica walls uncolored and thin. Lorica urn-shaped 8–14 μm length and 4–7 μm wide with pointed posterior and truncate and necked anterior end. Lorica surface possibly covered by bacteria. Cell ovoid with roundish posterior part. Starving cells not occupying half of lorica volume, satiated cells occupying a 2/3 of lorica chamber. Anterior flagellum about 1.5–2 times as long as cell. Nucleus median, lateral contractile vacuole situated in basal cell part. Numerous food vacuoles around cell periphery. Cysts not observed.

Found in the pond plankton samples (Borok, Yaroslavskaya Oblast, Russia). Noted from small freshwater bodies of the Yaroslavskaya Oblast. Known from pond samples of West Europe. Found in shallow waters of Rybinsk Reserve on filamentous algae (Zhukov, 1978). Also occurred in the lakes of Barentz Sea coast.

Bicosoeca griessmanni Bourrelly, 1951 (fig. 1, L–N).
= *B. pocillum* Griessmann, 1914

Solitary. Lorica cylindrical, with cone-shaped narrowing in basal part, colourless and without annular striation, 7–13 μm length and 4–7 μm wide. Pedicel absent. Lorica attached to the substrate by the pointed basal part directly. Cell oviform, 4–5 μm length, occupy a half or less of lorica volume and with a small groove at the anterior cell end. Apical flagellum about 2–2.5 times as long as the cell and may run up to 20–25 μm. Nucleus medial, lateral contractile vacuole situated in the basal part of the cell. Cysts not observed.

Found in a brackish-water lake of Kandalaksha Bay coast (White Sea). Marine species (Zhukov, 1993). Observed abundantly in algae cultures from Roskoff, France (Griessmann, 1914).

This species is similar to *Bicosoeca cylindrica* (Lackey, 1939) Bourrelly, 1951 (fig. 1, O), but differs by smaller lorica, more roundish lorica base and oval cell shape egg-shaped in *B. cylindrical* as well as by the absence of the bacteria covering the lorica of *B. cylindrica*.

Bicosoeca lacustris (Clark, 1968) Skuja, 1948 (fig. 1, P–R).

Lorica elliptical with pointed base and narrowed aperture, 8–16 μm long and 4.5–7.5 μm wide. Lorica walls colorless and thin. Cell ovoid, 5.5–7 μm long, 3–4 μm wide. Apical flagellum about 2–3 times as long as cell and usually reaching 25 μm. Nucleus medial, lateral contractile vacuole situated in basal part of cell. Cysts not observed.

This species was found in pond plankton samples (Borok, Yaroslavskaya Oblast, Russia). It is one of the most widespread heterotrophic flagellates (Kent, 1880); found

in small freshwater bodies of the Yaroslavskaya Oblast and sewage water plants (Tikhonenkov, 2006). It predominantly attaches to *Melosira, Asterionella, Stephanodiscus* in Rybinsk and other Volga reservoirs (Zhukov, 1979, 1993). It was recorded from estuarine waters and marine biotopes on artificial substrates of the White Sea (Railkin et al., 1990).

Other researchers noted smaller lorica dimensions of this species: 9–12 μm long and 4–5.5 μm wide (Zhukov, 1993). Short pedicel of *B. lacustris* attached lorica to the substrate was observed by some authors (Skuja, 1948). Old lorica usually has brown color (Skuja, 1948). This species is almost identical to *Bicosoeca kepneri* Reynolds, 1927 (fig. 1, S), but differs by more narrowed lorica base and low flexibility of lorica walls (Zhukov, 1978). It is also similar to *B. vacillans* Štolk, 1887, but differs by more elongated elliptical shape of the lorica and much shorter pedicel (or its total absence).

EXCAVATA

JAKOBIDA

HISTIONIDAE

Histiona aroides Pascher, 1943 (fig. 1, T–X)

Lorica transparent, annular structures invisible, scyphiform, narrowed to basis or very short pedicel attaching to substrats. Length of lorica 7–14 μm, breadth 4–9 μm. The top margin of lorica slightly bent inside. Shape of cell mostly irregular, less often — pear-shaped. Anterior part of cell forming cytoplasmic process (lip), having thicker and thiner parts (velum) transparent and slightly visible. Lip usually filled by food vacuoles. Two unequal length flagella co-located originate near the basis of lip. Long flagellum (13–20 μm) making comb-shaped movements and creating the current of water directed on velum. Small flagellum (7–10 μm) vibrating sporadically. Its top part setting against lip. This flagellum transferring bacteria to anterior part of lip and probably promoting their capture by cell. Large nucleus located in bottom part of cell and surrounded with granules. Contractile vacuole near flagellar base.

This species was found in the pond plankton samples (Borok, Yaroslavskaya Oblast, Russia). It occurred in stagnant reservoirs (Zhukov, 1993) and was noted from boggy lakes and detritus samples of the stagnant sites of Yaroslavskaya Oblast (Mylnikov, 1984; Tikhonenkov, 2006).

On the basis of earlier data (Mylnikov, 1984), the life cycle of this species consists of two vegetative stages (attached in lorica and floating form) and the rest stage. The moving stage is represented by more or less spindle-shaped floating forms without projections. Flagella make flapping movements. Moreover, the long flagellum rotates the distal part. Cells are attached to a substrate by the perinuclear end. Then, the lip appears and the lorica is formed. Encystment was observed for attached forms only. At that, the flagella discard and the cell becomes round. The cyst usually remains inside the lorica (5–6 μm in diameter). A thin cyst envelope with aperture stays at the lorica after excystation.

Pedicel that attach cell to the lorica is absent. The cell multiplies by short oblique division. This species differs from similar *H. velifera* (Voigt, 1902) Pascher, 1943, O'Kelly 1993 by lorica shape, which is conic or funnelform in *H. velifera* (fig. 1, Y).

Reclinomonas americana Flavin and Nerad, 1993 (fig. 1, Z–AB)

Lorica dish-shaped about 5–11 μm with thin colourless wall closely fitting cell. Lorica attached to substrate by very thin, perpendicular and indistinguishable pedicel. Cell crescent-shaped, 4–10 μm long. Ventral surface of cell with groove. Two acronematic flagella inserted at anterior end of cell. Long anterior free flagellum directed ven-

tro-posteriorly, about 10–16 μm long. Short posterior laterally directed flagellum lying along cytostomal groove and setting against cell margin, moving out distal end, making oscillation movements between margins of groove. Anterior flagellum vibrating and withdrawing bacteria to cell. Bacteria captured on surface of groove where food vacuoles formed. One of groove margins forming expansion (velum). Nucleus situated near flagellar basal part, contractile vacuole lying in posterior end of cell.

This species was found in the plankton samples from a water bod in Kanev Reserve (Ukraine). Noted from fresh waters of North America, New Zealand, Tasmania, Central Russia and Karelia as well as Antarctic freshwater lakes samples.

On the basis of earlier data (Mylnikov, Mylnikova, 2007) life cycle of this species consist of two vegetative stages (attached in lorica and floating form) and the rest stage. The floating cells have oval or cylindrical shape and two free flagella. Velum and cytostome groove are absent. The thin-walled cysts, which typically resided in the parent cell lorica, were spherical to slightly egg-shaped.

This species is similar to *R. campanula* (fig. 1, AC), however, the lorica of *R. campanula* has more elongate shape and long pedicel (Mylnikov, Mylnikova, 2007), which deviates from the lorica not at the right angle. Lorica walls of *R. campanula* (*Histiona campanula*) are not closely fitting the cell and well visible in a light microscope. Representatives of *Reclinomonas* differ from genus *Histiona* species by two good noticeable flagella and by the absence of elongated "lip", upward directed (Flavine, Nerad, 1993).

Discussion

Populations of the asexual organisms *per se* represent aggregations of some limited number of clones. Presence of continuum of forms and sizes is often a consequence of this phenomenon. Allocation of discrete species within the limits of a continuum becomes substantially relative and corresponds to methodological background of the researchers. This is not a general standpoint of definition of taxonomic significance of morphological characteristics. Similar problems characterize not only LHF taxonomy, but also systematics of many other groups of protists.

There are two opposite views on the asexual protist species concept. Some authors accept the concept of the wide or polytypic species (species *sensu lato*) and lump many "indistinguishable" species and forms into the "species complexes". In some cases, certainly, there are objective reasons for such lumping because of the absence of clear taxonomic diagnoses in many species and forms. The reasons for lumping are as follows. Firstly, many taxonomical features can easily change under the influence of various factors. For example, the shell of testate amoebae *Cyclopyxis kahli* may be composed on sand grains or diatom frustules depending on availability of building material in the environment (Korganova, 2004), whereas in many cases this character is used for species separation (compare *Difflugia bacillariarum* and *D. elegans* in Ogden, Hedley (1980)). Secondly, there is a wide spectrum of morphotypes arising in clonal cultures, which are usually described as separate species. In the first quarter of the XX century the studies of morphological variability of *Difflugia corona* clones, longtime modifications and variability of testaceans of the genus *Arcella* and *Centropyxis* showed that longtime impact of environmental factors affect heritable modifications in clonal cultures (e. g., Jollos, 1924). In some cases (Medioli et al., 1987) it was shown that in clonal culture of testate amoebae *Difflugia* the large amount of modifications can be formed, which are corresponding to 98 (!) separate species. W. Schönborn (1992) showed that under stable controlled conditions the variation coefficients of morphometrical parameters considerably grows with the time of conducting the clonal culture in laboratory experiments on testate amoebae clones *Trinema lineare* and *Euglypha laevis*.

Consequently, individual variability is likely to be genetically conditioned, and it is not always directly adaptive. In other words, spontaneous size fluctuations within certain intervals are contained in a genotype.

On the other hand, these is another approach, which lies in splitting of close related forms into different taxonomic units. This approach is highly applied in Centroheliozoa and testate amoebae. The splitting of closely related forms has an important ecological background. An investigation of ecological preferences of testate amoebae inhabiting sphagnum bogs (Bobrov et al., 2002) shows that closely related forms live in different microhabitat conditions. For example, three forms of *Trigonopyxis* inhabit microbiotopes with different moistening. The largest species *T. arcula major* dwell under the most moisture conditions, whereas the tiniest *T. minuta* in the driest ones. As for heterotrophic flagellate systematic, similar approach is observed in the groups of chrysomonads and thaumatomonads, whose taxonomy is based on the morphological peculiarities of cell scales, as well as systematics of heterotrophic euglenids for which a plenty of ecological data on the geographic distribution and biotic preferences are collected.

Recently, separation of specific complexes has been carried out on the base of molecular data, at that greatly differing DNA sequences of the same morphological species refer to one species complex, e. g., *Bodo saltans* species complex (e. g., von der Heyden, Cavalier-Smith, 2005). However, as the *B. saltans* species complex is studied in more detail, it probably needs to be divided into several species (von der Heyden, Cavalier-Smith, 2005).

The analysis of our species descriptions shows that the most essential taxonomic features of LHF external morphology are the shape, size, colour of the theca or lorica, as well as flagellum (flagella) length *vs.* cell length (diameter) ratio. The base light microscopy distinguishable cell organellas (nucleus and contractile vacuole) have similar cell localization both within species of the same genus and within different taxonomic groups (e. g. choanomonads and bicosoecids).

The analysis of original descriptions of investigated species shows that it is difficult to differentiate a clear morphological distinction between large amount LHF species. Especially it is traced in choanoflagellates taxonomy, where clear distinctions among genera are absent. It demonstrates necessity of the revision of both micro- and macrosystems of a group with detailed analysis of descriptions of XIX and beginning of XX centuries and clarification and revision of some genera and species taxonomy.

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